Internal models for motor control and trajectory planning

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A number of internal model concepts are now widespread in neuroscience and cognitive science. These concepts are supported by behavioral, neurophysiological, and imaging data; furthermore, these models have had their structures and functions revealed by such data. In particular, a specific theory on inverse dynamics model learning is directly supported by unit recordings from cerebellar Purkinje cells. Multiple paired forward inverse models describing how diverse objects and environments can be controlled and learned separately have recently been proposed. The 'minimum variance model' is another major recent advance in the computational theory of motor control. This model integrates two furiously disputed approaches on trajectory planning, strongly suggesting that both kinematic and dynamic internal models are utilized in movement planning and control.

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Abbreviations

DLPN	dorsolateral pontine nucleus
MST	medial superior temporal
OFR	ocular following responses
VPFL	ventral paraflocculus

Introduction

Internal models are neural mechanisms that can mimic the input/output characteristics, or their inverses, of the motor apparatus. Forward internal models can predict sensory consequences from efference copies of issued motor commands. Inverse internal models, on the other hand, can calculate necessary feedforward motor commands from desired trajectory information.

Fast and coordinated arm movements cannot be executed solely under feedback control, since biological feedback loops are slow and have small gains (Figure 1a). Thus, the internal model hypothesis (Figure 1b) proposes that the brain needs to acquire an inverse dynamics model of the object to be controlled through motor learning, after which motor control can be executed in a pure feedforward manner. In theory, a forward model of the motor apparatus embedded in an internal feedback loop can approximate an inverse model.

The internal model concept has its origin in control theory and robotics, but Ito [1] proposed almost 30 years ago that the cerebellum contains forward models of the limbs and other brain regions. More recently, internal models have attracted a broader range of specialists (e.g. neural network modelers, connectionists and neurophysiologists [2–4]), and have been studied increasingly seriously as one of the major theories of motor control and learning in neuroscience and cognitive science. Accordingly, in the past few years, much more direct and convincing data than ever before have been accumulated. Such data can already show the existence, structures, learning, functions and anatomy of internal models. Of particular importance, we have seen significant theoretical advances in elucidation of the generalization, multiplicity and switching of internal models, and their possible use in trajectory planning.

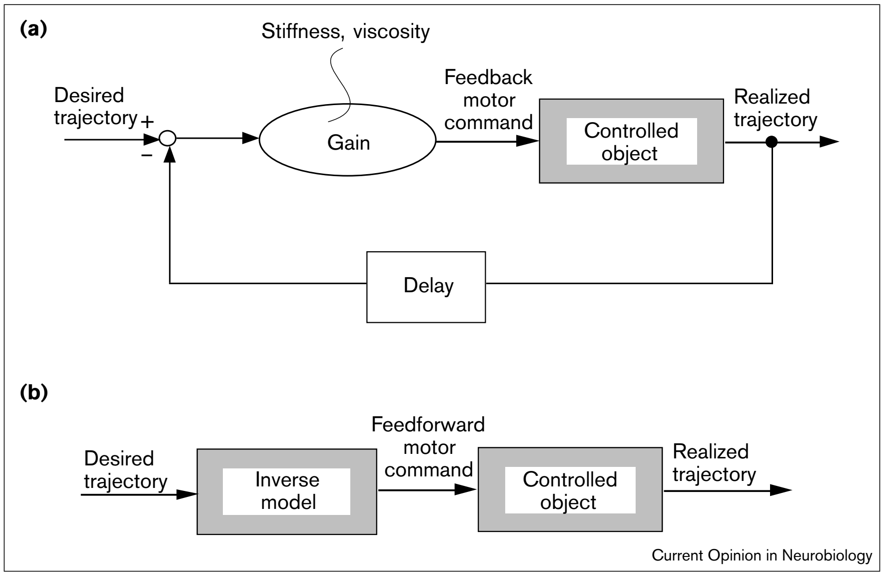
In this review, I will discuss data supporting the existence of internal models. It has been shown that the behavioral paradigms in use are diverse and include adaptation to force fields, posture control, grip-force–load-force coupling, oculomanual coordination, and the vestibular system. An explanation will be given on points of controversy between the equilibrium point control hypothesis and the internal model hypothesis, and some clues towards their resolution will be presented. Recent neurophysiological and imaging studies that suggest that the cerebellar cortex is a major site of internal models will also be discussed. Furthermore, structures of internal models will be explored by 'generalization' experiments; modularity and multiplicity are suggested by the data obtained. Finally, two major approaches to trajectory planning will be reviewed and a new theory will be introduced to integrate them.

Existence of internal models

When subjects first undertake point-to-point arm reaching movements under force fields which effectively change dynamic characteristics of the arm, their hand trajectories are distorted compared with the normal, roughly straight paths; also, the end point errors are large, especially in the direction of the applied force. The force fields generated predetermined forces which depended on the state space point (position, velocity), and were produced by a robot manipulandum [5] or by a rotating room [6,7•]. After repeated trials, the hand trajectories gradually become normal, straight paths, and the end point errors decrease in size. However, when the force fields are removed suddenly after this adaptation has occurred, the trajectories become distorted and the end-point errors become large in the opposite direction to the previously applied force. Such an occurrence can readily be explained as follows by the adaptation of the inverse dynamics model of the arm to the applied force field (see Figure 1b).

Under normal conditions, the inverse dynamics model calculates motor commands which appropriately compensate the arm dynamics. Under the altered dynamics conditions, in contrast, the motor commands are insufficient to compensate for the applied force, and this leads to distortions

Figure 1



Feedback and feedforward control using an inverse model of a controlled object. **(a)** In feedback control, the realized trajectory is compared with the desired trajectory, and the error is computed. The feedback motor command is generated from this error using a relatively simple algorithm, such as a proportional, integral and derivative feedback controller. In robotics, almost all practical applications depend solely on feedback controls. This is because feedback delays in artificial systems can be made small; hence, sampling and control frequencies can be quite high (from 500–10000 Hz). In biological motor control, however, the delay is very large. For visual feedback on arm movements, the delay ranges from 150–250 ms. Relatively fast spinal feedback loops still require 30–50 ms time delays. These are very large compared with the movement duration of very fast (150 ms) to intermediate (500 ms) movements. Because time delay occupies a large proportion of movement execution time, and feedback gains cannot be set high because of instability due to large delays, fast and smooth movements cannot be executed depending solely on feedback control. Muscle intrinsic mechanical properties produce proportional (stiffness) and derivative (viscosity) gains without delay. However, these viscoelasticities are small for well-trained movements [21,23•]. **(b)** If an inverse dynamics model is serially-connected with the controlled object, the serial system gives a mathematical identity function. That is, the output (i.e. the realized trajectory) is identical to the input (i.e. the desired trajectory). Thus, the inverse model, if it exists and can be learned, becomes an ideal feedforward controller. In biological systems with large feedback delays and small feedback gains, internal models are the only computational possibility for fast and well coordinated movements. Even for artificial robotic systems, if reduction gears are not used (e.g. direct drive motors, artificial muscles, hydraulic actuators), inverse models are required (see, for example, the URL http://www.erato.atr.co.jp/DB/).

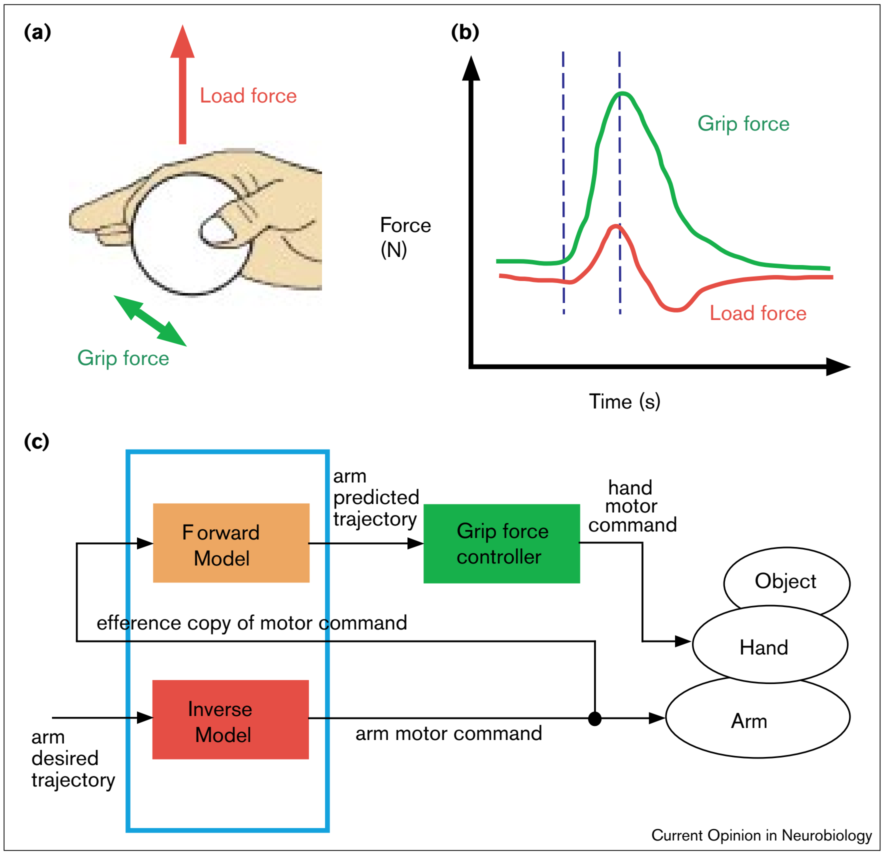
in the trajectories and large end-point errors. During repeated trials, the inverse dynamics model changes to the inverse of the combined arm dynamics and the applied force field. Then, normal trajectories reappear and the end-point errors are reduced. This adaptation is assumed to involve plastic changes of the synaptic efficacy of neurons constituting the inverse dynamics model. With the sudden removal of the applied force field, however, the inverse dynamics model continues to generate the motor commands to compensate for the arm dynamics, as well as the non-existing force field, and this leads to distortions in the trajectories in the opposite direction.

The most convincing set of data for the existence of forward models comes from studies on coordination between reaching and grasping. When an object is held with the tips of the index finger and thumb on either side (Figure 2a), the grip force is precisely controlled (Figure 2b) so that, under normal conditions, it is just slightly greater than the minimum grip force needed to prevent slip [8]; this is also so when the arm dynamics is altered by a robot [9]. Such a grip-force–load-force coupling is explained by a framework that contains both the inverse and forward models of the arm, as shown in Figure 2c. Functional magnetic resonance imaging (fMRI) studies have revealed cerebellar activity specific to grip-force–load-force coupling [10•], suggesting the existence of forward models in the cerebellum. In principle, the scheme shown in Figure 2c can be generalized to the coordination of any combined movements (e.g. eye and hand movement, or right-hand movement and left-hand movement) in any part of the body. Oculomanual coordination [11••], and bi-manual tracking (E Nakano, DM Wolpert, personal communications) are examples.

Internal models were also studied in the sensory system for processes other than motor control. The vestibular system is composed of semicircular canals, which report any angular acceleration, and otolith organs, which respond to any linear acceleration. Because the otolith responds to both the occurrence of linear acceleration and gravity, it is computationally difficult to analyse the ambiguous sensory information [12]. Through the use of dexterously designed vestibular stimuli and the examination of resulting eye movements in monkeys [13] and humans [14], internal models have been suggested to estimate linear acceleration and gravity from the canal and otolith outputs. This internal model can be classified as an inverse model of the sensor physics with acceleration and gravity as its inputs.

The necessity for internal models in motor control has been one of the central issues of debate in relation to equilibrium-point control. Muscle and peripheral reflex loops have spring-like properties that pull joints back to their equilibrium positions by generating a restoring force against external perturbations. This viscoelasticity can be regarded as peripheral feedback control gain, which is adjustable by regulating the associated muscle co-contraction level and reflex gain. It has been hypothesized that by exploiting this

Figure 2



Coordination of grip force and load force, and a computational model based on internal forward and inverse models. **(a)** When an object is held with the tips of the index finger and thumb on either side, the normal grip force on the contact surface allows for the development of a frictional force, which prevents the object from slipping. **(b)** The grip force is precisely controlled so that it is just slightly greater than the minimum grip force needed to prevent slip. **(c)** This grip-force–load-force coupling is explained by a framework that contains both the inverse and forward models of the arm. Take, for example, a point-to-point arm-reaching movement that takes place while the hand is grasping an object. The inverse model of the combined dynamics of the arm, hand and object calculates the necessary motor commands from the desired trajectory of the arm. These commands are sent to the arm muscles as well as to the forward dynamics model as the efference copy. Then, the forward model can predict an arm trajectory that is slightly in the future. Given the predicted arm trajectory, the load force is calculated; then, by multiplying a friction coefficient and a safety factor, the necessary minimum level of grip force can be calculated. To realize this grip force time course, motor commands are sent to hand muscles. This model predicts that three different computational elements are necessary for grip-force–load-force coupling: the inverse model for arm reaching; the forward model for arm trajectory prediction; and the grip force controller for grip execution. Tamada *et al.* (T Tamada *et al.*, personal communication) have recently identified three fMRI active loci corresponding to these three elements.

viscoelasticity, the brain can control the limbs simply by commanding a series of stable equilibrium positions aligned along the desired movement trajectory (i.e. the equilibrium-point control hypothesis) [15–17,18•]. In particular, it was once advocated that internal models are not necessary provided that the brain utilizes equilibrium control. This theory, however, requires that viscoelastic forces increase as the movement speeds up because the dynamic forces acting on the multijoint links grow in rough proportion to the square of the velocity. On the other hand, the alternative hypothesis (i.e. the internal model control, shown in Figure 1b), proposes the realization of a fast and accurate movement even with low viscoelastic forces. A point of controversy here is whether the CNS relies on high viscoelastic forces without internal models [15–17,18•] or utilizes acquired internal models with low viscoelastic forces [19–21,22•]. Recent observations of a relatively low stiffness during well-trained movements have supported the existence of internal models [21,23•].

Reports showing that the electromyogram (EMG) is higher in a novel environment than in a normal environment [24], however, have supported the empirical observation that any stiffness at the beginning of learning may not be as low as that after extensive training. Computational models have suggested that there is an advantage to integrating the muscle viscoelasticity and internal models for efficient learning of internal models [25,26]. Accordingly, one of the major future experimental objectives is to elucidate how these two schemes are integrated; Osu, Kato and Gomi have obtained new data suggesting a specific scheme of integration (R Osu, H Kato, H Gomi, personal communication).

Internal models in the cerebellum

It is conceivable that internal models are located in all brain regions having synaptic plasticity, provided that they receive and send out relevant information for their input and output. We have good reason to believe that at least some internal models are acquired and stored in the cerebellar cortex. For example, there is a new computational theory [27••] that allocates supervised learning, reinforcement learning, and unsupervised learning to the cerebellum, the basal ganglia and the cerebral cortex, respectively. This is partially based on previous cerebellar learning theories [28–30,31••]. The learning acquisition of internal models is best performed by supervised learning, and accordingly, the cerebellar cortex seems the most appropriate location as the storage site of internal models.

The most convincing neurophysiological data for internal models were obtained for eye movements. Kawano and his colleagues [32] studied neural circuits involved in controlling ocular following responses (OFR), which are reflex eye movements with a short latency. These circuits stabilize retinal images and are driven by large visual field movements. It is known that they involve the MST (medial superior temporal) area, dorsolateral pontine nucleus (DLPN), and the ventral paraflocculus (VPFL) of the cerebellum [32]. Figure 3 summarizes neural networks for OFR based on [32]; a similarity to the feedback–error–learning model [30] is suggested. In accordance with the theory, the climbing fiber inputs to Purkinje cells during OFR carry error signals in the motor command coordinates, and accordingly, their temporal waveforms can be well reproduced by the inverse dynamics model of the eye [33••]. In Figure 3, the simple spikes of the Purkinje cells during OFR are well fitted by the inverse dynamics model of the eye, but share an approximate mirror image relationship with the climbing fiber inputs. For both the climbing fibers and simple spikes, the position coefficients have the opposite sign to the real inverse dynamics model of the eye [34,35••], suggesting that the VPFL comprises a major, dynamic part of the inverse dynamics model, and also that other brain regions complement it. The data from monkeys could be strengthened by recording in the flocculus of cats during optokinetic responses [36•]. In particular, the negative sign of the position coefficient was confirmed, even with the inclusion of the slide term.

The MST area and DLPN send visual information to the VPFL [37], and drastic changes of neural codes occur at the parallel fiber Purkinje cell synapses. That is, in the area MST and DLPN, population coding is used: the optimum directions of the visual stimuli cover the entire 360° and the optimum velocities are widespread, and many different temporal waveforms of firings can be observed [32,37]. On the other hand, temporal rate coding is used for Purkinje cells: either downward or ipsilateral visual motion is optimal, the firing rate increases with the stimulus velocity, and the temporal waveform is stereotypically reconstructed by the inverse dynamics model. Computer simulations based on the feedback–error–learning theory [38,39] have shown that changes to neural codes, as well as the learning acquisition of the inverse dynamics model, can be reproduced based on the known synaptic plasticity of Purkinje cells, that is, long-term depression, long-term potentiation, and rebound potentiation.

Studying arm movements is much more difficult than studying eye movements with respect to the coordinate frame in which neural firings are encoded [40]. Accordingly, examining inverse dynamics representations is very difficult. However, strong physiological evidence suggests that the climbing fiber inputs also work to encode error signals for arm movements [41••]. In addition, imaging, physiological and lesion studies have demonstrated that the cerebellum is at least one of the possible sites for internal models for arm movements [42••,43••,44•,45•]. A theoretical model — that the cerebellum constitutes a major part of the parallel inverse models of the arm has been proposed [46••].

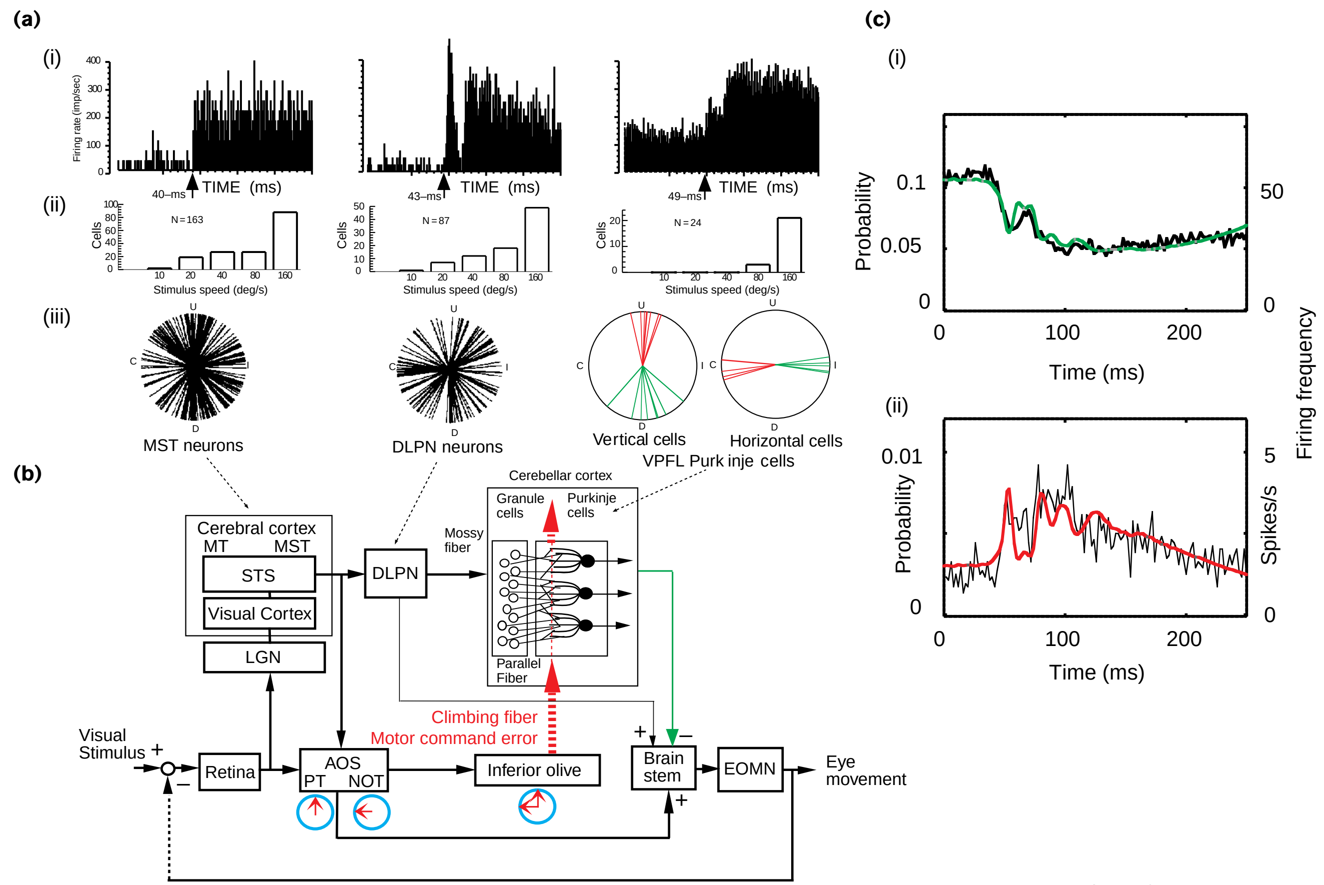
The most frustrating missing link in the cerebellar learning hypothesis is the computational clarification of peculiar physiological and anatomical characteristics of inferior olive neurons [47]. A compartmental biophysical model of inferior olive neurons electrically coupled by gap junctions has been found to reproduce many such physiological data both *in vivo* and *in vitro* [48••]. Furthermore, there has been a suggestion that there is 'desynchronization' of coupled neurons by gap junctions [48••]. This theoretical work may in fact provide an important clue towards elucidating the computational significance of the above missing link (N Schweighofer, K Doya, M Kawato, unpublished data).

Structures of internal models

The functional structures of internal models can be probed by the so-called 'generalization experiment' [49–52,53•,54,55•]. Humans or animals are trained for a specific set of movement trajectories with an altered kinematic or dynamic perturbation. After sufficient learning, the organism's ability to cope with different trajectories or movements in a different part of the workspace in which the motor apparatus can move is examined. If 'generalization' is considered perfect, new trajectories are controlled precisely from the beginning. If generalization is considered to not exist, the performance of subjects undergoing new experiences is as poor as those with no prior learning. The brain does not memorize a simple association between movement instances and motor commands. Rather, it has an internal memory of the motor apparatus and the external world in the form of an inverse dynamics model with state–space representations. The motor commands at each instance are calculated by a functional map from the state–space input point, including the acceleration, velocity, and position of the desired trajectory [51,52]. If generalization of learning is perfect, the inverse dynamics model after learning is very precise over the entire state–space, and must therefore take the form of a parametric and analytical model. In contrast, if there is no generalization apart from the experienced trajectory, the inverse dynamics model is a local table-look-up map. The experimental data [49–52,53•,54,55•] suggests neither is the case. Instead, an intermediate generalization level has been consistently reported. It is possible, therefore, that internal models in the brain are similar to artificial neural networks or connectionist models in their generalization capability.

An imperfect generalization of internal models would strongly suggest the need for modular structures [56]. This

Figure 3



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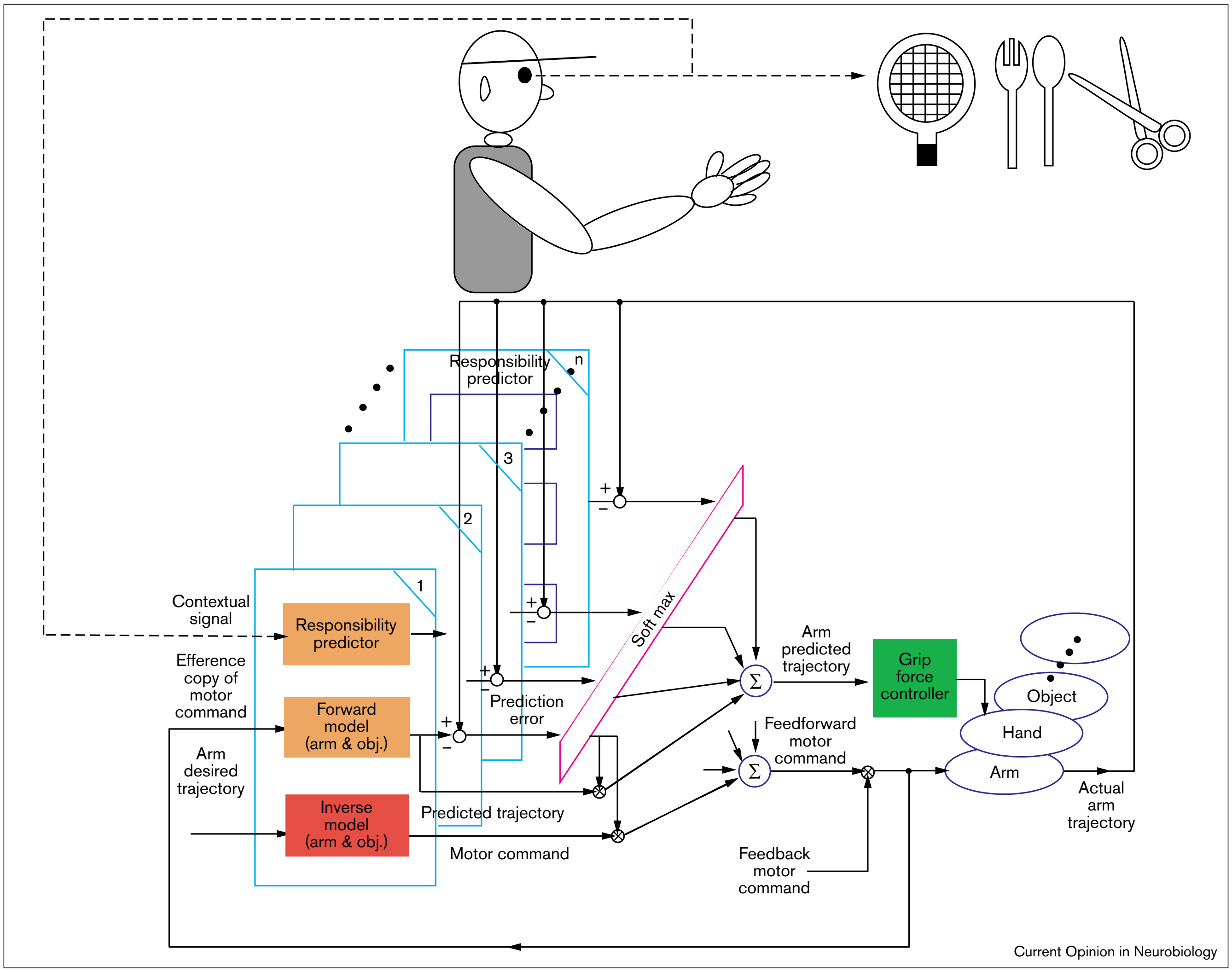
Change of neural codes and learning of inverse dynamics model in the cerebellum for OFR. The neurophysiological data shown in (a) and (c) are taken from [32,33••,37] and reproduced with permission. (a) The firing characteristics of MST, DLPN and VPFL neurons. (b) A schematic neural circuit for OFR. (c) Temporal firing patterns of VPFL Purkinje cells in upward eye movements induced by upward visual motion. **(a)** (i) Peri-stimulus time graphs of the firing rates of a typical neuron in each of the three areas. The origin of time is taken as the onset of visual stimulus motion. (ii) Histograms of a number of cells within a given range of the optimum stimulus speeds. (iii) Polar plots of optimum stimulus directions. U, C, D and I indicate upward, contralateral, downward, and ipsilateral, respectively. VPFL Purkinje cells were classified into two groups, vertical cells and horizontal cells, based on simple spike (green) and complex spike (red) optimum directions. **(b)** The circuit can be divided into two main pathways. The upper part shows the cortico–cortical (the cerebral cortex to the cerebellar cortex) pathway, which corresponds to the feedforward arc of the feedback–error–learning model. The lower part of the pathway shows the phylogenetically older feedback pathway containing the accessory optic system, which corresponds to a crude feedback controller in the feedback–error–learning scheme. The theory predicts that the accessory optic system first determines the motor command coordinates (upward for PT [pretectum], and contralateral for NOT [nucleus of optic tract]). This motor frame of reference is conveyed to the inferior olive nucleus, and determines the optimum stimulus directions of the climbing fiber responses, which are reflected in complex spikes (aiii, red lines). Based on known synaptic plasticity (long-term depression, long-term potentiation, rebound potentiation) of Purkinje cells, it is predicted that the optimum stimulus direction of each Purkinje cell for simple spikes and complex spikes is 180° opposite. (aiii, right shows that this is the case). **(c)** Accumulated temporal firing patterns of nine Purkinje cells (black curves) and their reconstruction based on inverse dynamics model (red and green curves). The model further predicts that the temporal firing patterns of (i) simple spikes and (ii) complex spikes should be mirror images of each other. Kobayashi *et al.* [33••] confirmed this, and furthermore reconstructed simple spike as well as complex spike firing waveforms by the inverse dynamics model. This strongly supports the most critical assumption of the feedback–error–learning scheme that the climbing fiber inputs convey error signals in the motor command coordinates, and the simple spike firing is learned by being guided by this error signal through synaptic plasticity. Yamamoto *et al.* [38,39] reproduced the dramatic change of neural codes, and the learning acquisition of simple spike firing patterns, as well as eye movement waveforms based on Purkinje cell synaptic plasticity. AOS, accessory optic system; EOMN, extraocular motor neuron; LGN, lateral geniculate nucleus; MT, middle temporal area; STS, superior temporal sulcus.

is because a single gigantic internal model with an imperfect generalization capability cannot possibly learn or deal with a whole range of different behavioral situations. However, different modules cannot be entirely independent from one another because they all exhibit some degree of generalization. This means that some interference may occur between multiple internal models unless an efficient computational mechanism exists to regulate

Figure 4



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Multiple paired forward and inverse models (MPFIMs) [62••] in the context of grip-force–load-force coupling for multiple manipulated objects. The computational scheme shown in Figure 2 is fine as long as only a single object is manipulated. But a single internal model cannot deal with a large number of objects with different kinematic and dynamic properties. This is because incomplete learning generalization leads to a catastrophic interference between different learning epochs and between different motor primitives. MPFIM postulates a computationally coherent principle to overcome this difficulty. The brain prepares many modules, each of which comprises three elements: a forward model, an inverse model, and a responsibility predictor. Learning, switching and blending of these multiple modules are, in principle, controlled by the relative goodness of predictions made by many forward models. Furthermore, predictive switching between modules is performed by responsibility predictors based on contextual information. In the Bayesian framework, the outputs from the responsibility predictors determine prior probability about which module will be recruited for a given environmental situation, and the prediction error of each forward model determines which module is likely to be appropriate for the situation. A soft max function, gathering all products of the prior probability and the likelihood, finally computes the responsibility signal (0–1), which specifies the control contribution of the inverse model, as well as the learning responsibility of inverse and forward models within each module. For example, suppose that a person needs to manipulate one of several objects (see upper inset). By visual information of the object, an appropriate module for, say, a racket could be pre-selected. On actual manipulation of the object, the forward model for the racket module predicts sensory consequence from the efference copy of issued motor commands. If its prediction is good, that module will continue to be used. However, if the visual information is erroneous and the object actually grasped is a fork, the racket module prediction is bad and the fork module prediction is better, thus the racket module will be turned off and the fork module will be turned on after actual movement execution. Haruno *et al.* [63••] simulated a simple version of this ‘size–weight illusion’. Contextual information for the responsibility predictor could be virtually anything useful, such as vision, audition, tactile information, reasoning, verbal instruction, sequence of movement elements, outputs from other responsibility predictors, descending signals from higher brain regions, and so on. This gives versatile cognitive capability to MPFIM. From previous studies on the interference of two learning epochs [51,52,57,58], we infer that if some contextual signal is very unusual and consequently strong (e.g. a unique combination of tactile and visual information if an arm is attached to a robotic manipulandum), other contextual signals have smaller influences (e.g. color is too weak, but posture and time still have discriminating effects). Because MPFIM introduces a blending of multiple inverse dynamics model (IDM) inputs, a finite number of modules could in principle deal with a vast number of different objects (see simulation [63••], as well as supporting behavioral studies [59,61••]).

their learning and involvement in a specific situation. Different internal models do seem to compete with each other in learning, especially for events involved in temporal proximity [57,58]. Interestingly, it has been found that multiple internal models can be mixed in an adaptive way when necessary [59,60••,61••].

On the basis of the findings described above, a new theory has recently been developed where multiple internal models can be learned and combined adaptively [62••,63••]. Figure 4 shows how this new theory can be used to explain the manipulation of many different objects with a finite number of internal model modules, while at the same time efficiently utilizing contextual information such as the vision of objects, verbal instructions, or the sequence of object presentation.

Trajectory formation

Computational theories on how arm reaching trajectories are planned have been a central issue in motor control since it was shown that they involve roughly straight hand paths and bell-shaped velocity profiles [64]. Many of the different computational models can be classified into two types: kinematic models such as the minimum jerk model [65], and dynamic models such as the minimum torque-change model [66]. Because these two classes of models enable the experimental testing of qualitatively different predictions, rich data sets are now available for discriminating between the two types (for kinematic planning and against dynamic planning, see [67–70]; for dynamic planning and against kinematic planning, see [71,72•,73•,74••]). However, analyses have been complicated and there remain areas of controversy [75].

The integration of these two approaches has been suggested [76•], and an ingenious theory of integration was recently proposed by Harris and Wolpert [77••]. Their minimum variance model also takes the form of an optimization model, in the tradition of many previous models. The objective for optimization in this model is to minimize the end point variance, and is therefore a purely kinematic variable. This variance, however, critically depends on the magnitude of the motor commands. Consequently, the whole optimization process is completely dynamic — that is, the optimal trajectory critically depends on the dynamics of the muscles involved, the motor apparatus, and the environment.

The 'minimum variance model' is thus kinematic in its objective function, but the computational process is dynamic, and the trajectory depends on the dynamics. This model can be viewed as a version of the minimum motor command change model [75]. This is because in the integral of the objective function, the square of the motor commands is increasingly more heavily weighted as the time approaches the movement end. Finally, because the computational process takes into account both the kinematics and dynamics of the motor task, it is important for both kinematic and dynamic internal models to be utilized for the trajectory planning, either implicitly or explicitly.

Conclusions

The concepts concerning internal models have now been well supported by behavioral studies in the field of sensory motor control. Neurophysiological studies have just begun but should be fruitful in the next five years. Theoretically, the concept should be extended from pure sensory motor control to cognitive domains as we have a flood of data suggesting cerebellar involvement in higher cognitive functions such as language [78,79,80••]. This is especially important because the cerebellar computational principle can be ubiquitous, on the basis of the uniform neural circuit of the cerebellar cortex, despite diverse functions of different cerebellar loci. In the near future, the author expects major breakthroughs in the concepts and computational theories of internal models entering into cognitive domains such as communication, thinking, and consciousness, on the basis of their firm foundations in sensory motor integration.

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Ito M: **Neurophysiological aspects of the cerebellar motor control system.** *Int J Neurol* 1970, **7**:162-176.

2. Kawato M, Furawaka K, Suzuki R: **A hierarchical neural network model for the control and learning of voluntary movements.** *Biol Cybern* 1987, **56**:1-17.

3. Jordan MI, Rumelhart DE: **Forward models: supervised learning with a distal teacher.** *Cogn Sci* 1992, **16**:307-354.

4. Miall RC, Weir DJ, Wolpert DM, Stein JF: **Is the cerebellum a Smith Predictor?** *J Motor Behav* 1993, **25**:203-216.

5. Shadmehr R, Mussa-Ivaldi FA: **Adaptive representation of dynamics during learning of a motor task.** *J Neurosci* 1994, **14**:3208-3224.

6. Lackner JR, Dizio P: **Rapid adaptation to Coriolis force perturbations of arm trajectory.** *J Neurophysiol* 1994, **72**:299-313.

7. • Lackner JR, Dizio P: **Gravitoinertial force background level affects adaptation to Coriolis force perturbations of reaching movements.** *J Neurophysiol* 1998, **80**:546-553.

In a rotating room environment [6], the transient, movement-dependent Coriolis forces and the static centrifugal forces were generated, and their combined effects on the adaptation of reaching movements toward a just-extinguished visual target were examined. An increase in background force level above normal gravity did not affect the adaptation to restore the straight paths, but did hinder restoration of reaching accuracy. This suggests that the inverse dynamics model for trajectory control and the inverse statics model for posture maintenance are anatomically separate.

8. Johansson RS, Westling G: **Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects.** *Exp Brain Res* 1984, **56**:550-564.

9. Flanagan JR, Wing AM: **The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads.** *J Neurosci* 1997, **17**:1519-1528.

10. • Tamada T, Miyauchi S, Imamizu H, Yoshioka T, Kawato M: **Activation of the cerebellum in grip force and load force coordination: an fMRI study.** *Neuroimage* 1999, **6**:S492.

Functional magnetic resonance imaging activation during hand movements while grasping an object in precision grip was found to be larger than during power grip in the lateral cerebellum. In consideration of the computational model of grip-force–load-force coupling shown in Figure 2, which is necessary only for the precision grip, it is suggested that a forward model of the object is located in the cerebellum.

11. •• Scarchilli K, Vercher JL: **The oculomanual coordination control center takes into account the mechanical properties of the arm**. *Exp Brain Res* 1999, **124**:42-52.

When the eyes tracked a target that was controlled by an arm movement, the smooth pursuit latency was 0 ms whereas it was 150 ms for an external target. When an electromagnetic brake impeded the arm motion unexpectedly, the eye movement phase led the target motion. This strongly supports the coordination model shown in Figure 2, originally developed for grip–force–load–force coupling. In the figure, the grip force controller should be replaced by the smooth pursuit controller.

12. Snyder L: **This way up: illusions and internal models in the vestibular system.** *Nat Neurosci* 1999, **2**:396-398.

13. Hess BJ, Angelaki DE: **Oculomotor control of primary eye position discriminates between translation and tilt.** *J Neurophysiol* 1999, **81**:394-398.

14. Merfeld DM, Zupan L, Peterka RJ: **Humans use internal models to estimate gravity and linear acceleration.** *Nature* 1999, **398**:615-618.

15. Feldman AG: **Functional tuning of nervous system with control of movement or maintenance of a steady posture. 2. Controllable parameters of the muscles.** *Biophysics* 1966, **11**:565-578.

16. Bizzi E, Accornero N, Chapple W, Hogan N: **Posture control and trajectory formation during arm movement.** *J Neurosci* 1984, **4**:2738-2744.

17. Flash T: **The control of hand equilibrium trajectories in multi-joint arm movements.** *Biol Cybern* 1987, **57**:257-274.

18. • Gribble PL, Ostry DJ, Sanguineti V, Laboissiere R: **Are complex control signals required for human arm movement?** *J Neurophysiol* 1998, **79**:1409-1424.

The data of [21] were reinterpreted by an equilibrium control hypthosesis with a straight equilibrium trajectory. However, the dynamics of the robotic manipulator used in the experiment was neglected, and the complicated muscle model used was not quantitatively validated (see annotation [74••]).

19. Latash ML, Gottlieb GL: **Reconstruction of shifting elbow joint compliant characteristics during fast and slow movements.** *Neuroscience* 1991, **43**:697-712.

20. Katayama M, Kawato M: **Virtual trajectory and stiffness ellipse during multijoint arm movement predicted by neural inverse models.** *Biol Cybern* 1993, **69**:353-362.

21. Gomi H, Kawato M: **Equilibrium-point control hypothesis examined by measured arm-stiffness during multi-joint movement.** *Science* 1996, **272**:117-120.

22. • Gribble PL, Ostry DJ: **Compensation for interaction torques during single and multi-joint limb movement.** *J Neurophysiol* 1999, **82**:2310-2326.

The authors confirmed the conclusion of previous studies [19–21] that the equilibrium trajectory, if it is used in the brain, cannot be straight by examining EMG signals. Compare with conclusions from [18•].

23. • Morasso PG, Schieppati M: **Can muscle stiffness alone stabilize upright standing?** *J Neurophysiol* 1999, **82**:1622-1626.

The authors showed that intrinsic muscle stiffness is not strong enough to stabilize upright posture. Usage of internal models was suggested as the alternative.

24. Milner TE, Cloutier C: **Compensation for mechanically unstable loading in voluntary wrist movement.** *Exp Brain Res* 1993, **94**:522-532.

25. Sanger TD: **Neural network learning control of robot manipulators using gradually increasing task difficulty.** *IEEE Trans Robotics Automat* 1994, **10**:323-333.

26. Katayama M, Inoue S, Kawato M: **A strategy of motor learning using adjustable parameters for arm movement.** *Proceedings of the 20th Annual International Conference of the IEEE Engineering in Medicine and Biology Society*; 29 Oct–1 Nov 1998, Hong Kong. IEEE; 1998:2370-2373.

27. •• Doya K: **What are the computations of cerebellum, basal ganglia, and cerebral cortex?** *Neural Networks* 1999, **12**:961-974.

A new, large-scale theory is proposed to explain how the three brain regions – the cerebral cortex, the basal ganglia and the cerebellum – collaborate to solve difficult behavioral learning problems. Computationally, these three regions were characterized by unsupervised learning, reinforcement learning and supervised learning, respectively.

28. Marr D: **A theory of cerebellar cortex.** *J Physiol* 1969, **202**:437-470.

29. Albus JS: **A theory of cerebellar function.** *Math Biosci* 1971, **10**:25-61.

30. Kawato M, Gomi H: **The cerebellum and VOR/OKR learning models.** *Trends Neurosci* 1992, **15**:445-453.

31. •• Thach WT: **A role for the cerebellum in learning movement coordination.** *Neurobiol Learn Mem* 1998, **70**:177-188.

This is a review of the author's brilliant contributions to the elucidation of cerebellar functions in motor learning and coordination. A proposed cerebellar theory of coordination between different degrees of freedom by the use of long parallel fibers was a large leap forward from the classical Marr–Albus–Ito theory, and is very closely related to internal model theories in computational essence.

32. Kawano K, Takemura A, Inoue Y, Kitama T, Kobayashi Y, Mustari MJ: **Visual inputs to cerebellar ventral paraflocculus during ocular following responses.** *Prog Brain Res* 1996, **112**:415-422.

33. •• Kobayashi Y, Kawano K, Takemura A, Inoue Y, Kitama T, Gomi H, Kawato M: **Temporal firing patterns of Purkinje cells in the cerebellar ventral paraflocculus during ocular following responses in monkeys. II. Complex spikes.** *J Neurophysiol* 1998, **80**:832-848.

Although the firing rates of Purkinje cell complex spikes are very low, when many trials were averaged during ocular following responses, their temporal firing patterns conveyed high-frequency and smooth waveforms which were well reconstructed from a linear combination of acceleration, velocity and position of eye movement. This supports the most critical assumption of the cerebellar feedback–error–learning theory [2] that climbing fiber inputs carry error signals in the motor command coordinates.

34. Shidara M, Kawano K, Gomi H, Kawato M: **Inverse-dynamics model eye movement control by Purkinje cells in the cerebellum.** *Nature* 1993, **365**:50-52.

35. •• Gomi H, Shidara M, Takemura A, Inoue Y, Kawano K, Kawato M: **Temporal firing patterns of Purkinje cells in the cerebellar ventral paraflocculus during ocular following responses in monkeys. I. Simple spikes.** *J Neurophysiol* 1998, **80**:818-831.

The simple spike firing patterns of Purkinje cells were well reconstructed from a linear combination of acceleration, velocity and position of eye movement under various stiumulus conditions. The findings of an earlier report [34] was strengthened by the examination of a larger number of cells and a larger number of stimulus conditions. In combination with [37], this suggests that the cerebellar cortex is a major site of the inverse dynamics model of the eye.

36. • Kitama T, Omata T, Mizukoshi A, Ueno T, Sato Y: **Motor dynamics encoding in cat cerebellar flocculus middle zone during optokinetic eye movements.** *J Neurophysiol* 1999, **82**:2235-2248.

A similar technique to those of [34,35••] was applied to cat flocculus during optokinetic eye movements. The results not only confirmed previous studies but also strengthened the negative coefficient of the position even when the slide term, that is the time derivative of the firing rates, is included in the linear regression.

37. Takemura A, Inoue Y, Gomi H, Kawato M, Kawano K: **Analysis of neuronal activities during ocular following responses in alert monkeys.** *Tech Rep IEICE* 1999, **NC99-22**:77-84.

38. Yamamoto K, Kobayashi Y, Takemura A, Kawano K, Kawato M: **A mathematical model that reproduces vertical ocular following responses from visual stimuli.** *Neurosci Res* 1997, **29**:161-169.

39. Yamamoto K, Kobayashi Y, Takemura A, Kawano K, Kawato M: **A computational simulation on the adaptation of vertical ocular following responses.** *Tech Rep IEICE* 1998, **NC97-131**:229-236.

40. Ebner TJ: **A role for the cerebellum in the control of limb movement velocity.** *Curr Opin Neurobiol* 1998, **8**:762-769.

41. •• Kitazawa S, Kimura T, Yin P: **Cerebellar complex spikes encode both destinations and errors in arm movements.** *Nature* 1998, **392**:494-497.

What is actually represented by cerebellar complex spikes had been much less understood for arm movements than for eye movements. This study, by utilizing a sophisticated information measure, clearly revealed that the complex spikes in monkey multijoint arm movements represent errors in motor performance at the end of movement. Their coding of the target location at the beginning of movement can also be interpreted as the predicted error for a default movement response, as simulated in [46••].

42. Imamizu H, Miyauchi S, Tamada T, Sasaki Y, Takino R, Putz B,
•• Yoshioka T, Kawato M: **Human cirebellar activity reflecting an aquired internal model of a novel tool.** *Nature* 1999, in press.

Previous neuroimaging studies reported a decrease in cerebellar activities along with motor or cognitive learning. These results have often been interpreted as suggesting that the cerebellum is important only in the early phase of learning and that it is not the memory site. In these interpretations, the internal models are not located in the cerebellum. The authors showed that cerebellar activity remains even after sufficient learning by dexterously equalizing error levels between the test and control conditions.

43. Blakemore SJ, Wolpert DM, Frith CD: **Central cancellation of self**
•• **produced tickle sensation.** *Nat Neurosci* 1998, **1**:635-640.

Self-produced tickling is not as amusing as tickling by others. The authors found decreased cerebellar activity during tickling by oneself than during the same movements which did not produce tickling, and further decreased activity compared with externally produced tickling. Cancellation of the sensory inputs by predictions of sensory consequences from the efference copy of the motor commands using the forward model is suggested. This is attractive since complex spikes, probably the most energy-demanding processes in the cerebellar cortex [42••], were known to be activated by unexpected events but not by physically equivalent but predictable events. It is still puzzling why the cerebellar activity during self-produced tickling is lower than the rest condition. Simple cancellation can explain activity negation, but cannot explain activity reduction.

44. Miall RC, Keating JG, Malkmus M, Thach WT: **Purkinje cell complex**
• **spikes are predicted by simple spike activity.** *Nat Neurosci* 1998, **1**:13-15.

Mean simple spike firing rates triggered by a complex spike during intertask intervals of monkey cerebellum were examined. It was found that the simple spike firing rates about 150 ms before the complex spike occurrence were statistically larger than background. This could be interpreted in the framework of the forward model predicting sensory consequences. The simple spikes make predictions about future sensory events, and these are compared with the real sensory feedback after a 150 ms sensory time delay; their consequences are represented as complex spikes.

45. Baizer JS, Kralj-Hans I, Glickstein M: **Cerebellar lesions and prism**
• **adaptation in macaque monkeys.** *J Neurophysiol* 1999, **81**:1960-1965.

It was suggested that the cerebellum is involved in prism adaptation because lesion of almost all of the cerebellar cortex, which receives mossy fiber visual inputs, abolished prism adaptation capability in a monkey. Internal models for prism adaptation could also be located in the cerebellum.

46. Schweighofer N, Spoelstra J, Arbib MA, Kawato M: **Role of the**
•• **cerebellum in reaching quickly and accurately. II. A detailed model of the intermediate cerebellum.** *Eur J Neurosci* 1998, **10**:95-105.

This is a simulation study of the learning inverse dynamics model of the arm in the intermediate cerebellum based on the feedback–error–learning model. Realistic time delays were assumed and the inverse model was distributed over the cerebellum and the cerebral cortex.

47. De Zeeuw CI, Simpson JI, Hoogenraad CC, Galjart N, Koekkoek SK, Ruigrok TJ: **Microcircuitry and function of the inferior olive.** *Trends Neurosci* 1998, **21**:391-400.

48. Schweighofer N, Doya K, Kawato M: **Electrophysiological properties**
•• **of inferior olive neurons: a compartmental model.** *J Neurophysiol* 1999, **82**:804-817.

A detailed biophysical model of an inferior olive neuron was developed. The model comprises the soma and the dentritic compartments, and is based on known spatial distributions of gap junctions and diverse ionic conductances. The model reproduced many peculiar characteristics found in electrophysiological experiments *in vitro*. Most surprisingly, it showed that electrical junctions have desynchronization effects on coupled inferior olive neurons for a wide range of parameters.

49. Imamizu H, Uno Y, Kawato M: **Internal representation of motor apparatus: implications from generalization in visuo-motor learning.** *J Exp Psychol [Hum Percept Perform]* 1995, **21**:1174-1198.

50. Ghahramani Z, Wolpert DM, Jordan MI: **Generalization to local remappings of the visuomotor coordinate transformation.** *J Neurosci* 1996, **16**:7085-7096.

51. Gandolfo F, Mussa-Ivaldi FA, Bizzi E: **Motor learning by field approximation.** *Proc Natl Acad Sci USA* 1996, **93**:3843-3846.

52. Conditt MA, Gandolfo F, Mussa-Ivaldi FA: **The motor system does not learn the dynamics of the arm by rote memorization of past experience.** *J Neurophysiol* 1997, **78**:554-560.

53. Sainburg RL, Ghez C, Kalakainis D: **Intersegmental dynamics are**
• **controlled by sequential anticipatory, error correction, and postural mechanisms.** *J Neurophysiol* 1999, **81**:1045-1055.

Previous adaptation studies introduced force fields that are dependent only on velocity and position (e.g. viscous force fields, Coriolis forces, spring force fields), but inertial force fields were difficult to implement even with a high-performance robotic manipulandum. The authors utilized an air sled system and an off-axis load to introduce an interesting novel inertial force field. Generalization of learning was limited to a small range of direction angles, which is in accordance with previous studies using viscous force fields [51,52] or kinematic rotation [49].

54. Kitazawa S, Kimura T, Uka T: **Prism adaptation of reaching movements: specificity for the velocity of reaching.** *J Neurosci* 1997, **17**:1481-1492.

55. Goodbody SJ, Wolpert DM: **Temporal and amplitude generalization**
• **in motor learning.** *J Neurophysiol* 1998, **79**:1825-1838.

A viscous, rotating-type force field was applied by a robotic interface to the arm. Subjects were trained with a reaching movement having a specific amplitude and duration. Then, generalization was examined for different durations and amplitudes. Most surprisingly, and in contrast to almost all previous studies (particularly [54]), generalization was best modeled by a linear map – that is, generalization was global rather than local. It is possible that parallel fiber inputs to the cerebellum encode velocity information by their firing rates while other information, such as position and direction, is encoded by population coding. Thus, we expect good generalization only for velocities because only velocity-dependent terms are represented linearly in Purkinje cell outputs on this assumption.

56. Jacobs RA, Jordan MI, Nowlan SJ, Hinton GE: **Adaptive mixtures of local experts.** *Neural Comp* 1991, **3**:79-87.

57. Shadmehr R, Brashers-Krug T: **Functional stages in the formation of human long-term motor memory.** *J Neurosci* 1997, **17**:409-419.

58. Shadmehr R, Holcomb HH: **Inhibitory control of competing motor memories.** *Exp Brain Res* 1999, **126**:235-251.

59. Ghahramani Z, Wolpert DM: **Modular decomposition in visuomotor learning.** *Nature* 1997, **386**:392-395.

60. Blakemore SJ, Goodbody SJ, Wolpert DM: **Predicting the**
•• **consequences of our own actions: the role of sensorimotor context estimation.** *J Neurosci* 1998, **18**:7511-7518.

Two robots simulated a case in which virtual objects were held in one hand and acted on by the other. Precise predictive grip-force modulation of the restraining hand was observed only when the force feedback gain between the two robots was close to 1, just like with a real object. The results show that predictive grip-force modulation requires not only self-generated movements but also a sensory consequence which is consistent with a specific context. That is, if the forward model's prediction in Figure 2 is not good, that coordination scheme is not used. The authors proposed the conceptual model, which led to the basic idea of determining the responsibility of each module by the goodness of the prediction of the forward model within that module [62••].

61. Flanagan R, Nakano E, Imamizu H, Osu R, Yoshioka T, Kawato M:
•• **Composition and decomposition of internal models in motor learning under altered kinematic and dynamic environments.** *J Neurosci* 1999, **19**:Rapid Communication 34:1-5.

Multiplicity of internal models for dynamic and kinematic transformations was investigated in order to determine whether multiple internal model can be composed or decomposed when occasion calls. When subjects learned a visuomotor rotation and viscous curl field first, reaching errors were smaller for a combination of these transformation than without prior experiences.

62. Wolpert DM, Kawato M: **Multiple paired forward and inverse**
•• **models for motor control.** *Neural Networks* 1998, **11**:1317-1329.

It was postulated that the best way to control learning and the contributions of different motor primitives (controllers, or inverse models) is to use the prediction goodness of corresponding predictors (forward models). This basic idea, strengthened by a responsibility predictor, provides an attractive Bayesian framework to explain rich behaviors in complicated environments.

63. Haruno M, Wolpert D, Kawato M: **Multiple paired forward-inverse**
•• **models for human motor learning and control**. In *Advances in Neural Information Processing Systems,* 11. Edited by Kearns MS, Solla SA, Cohn DA. Cambridge: MIT Press; 1999:31-37.

This describes mathematical and simulation studies examining the basic idea proposed in [62••]. Multiple pairs of forward and inverse models were automatically acquired for different behavioral situations. A finite number of multiple models were shown to be able to deal with a much larger number of situations. The 'size–weight illusion' was also simulated.

64. Abend W, Bizzi E, Morasso P: **Human arm trajectory formation.** *Brain* 1982, **105**:331-348.

65. Flash T, Hogan N: **The coordination of arm movements: an experimentally confirmed mathematical model.** *J Neurosci* 1985, **5**:1688-1703.

66. Uno Y, Kawato M, Suzuki R: **Formation and control of optimal trajectory in human multijoint arm movement — minimum torque-change model.** *Biol Cybern* 1989, **61**:89-101.

67. Flanagan JR, Rao AK: **Trajectory adaptation to a nonlinear visuomotor transformation: evidence of motion planning in visually perceived space.** *J Neurophysiol* 1995, **74**:2174-2178.

68. Wolpert DM, Ghahramani Z, Jordan MI: **Perceptual distortion contributes to the curvature of human reaching movements.** *Exp Brain Res* 1994, **98**:153-156.

69. Wolpert DM, Ghahramani Z, Jordan MI: **Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study.** *Exp Brain Res* 1995, **103**:460-470.

70. Okadome T, Honda M: **Kinematic construction of the trajectory of sequential arm movements.** *Biol Cybern* 1999, **80**:157-169.

71. Osu R, Uno Y, Koike Y, Kawato M: **Possible explanations for trajectory curvature in multijoint arm movements**. *J Exp Psychol [Hum Percept Perform]* 1997, **23**:890-913.

72. Todorov EV, Jordan MI: **Smoothness maximization along a**
• **predefined path accurately predicts the speed profiles of complex arm movements.** *J Neurophysiol* 1998, **80**:696-714.

The authors proposed a constrained optimization model to explain known regularities between velocity profiles and hand path curvature. For an observed path of the hand in space, the velocity profile along that path will be the one that minimizes jerk. This model explains the data better than the 2/3 power-law.

73. Sabes PN, Jordan MI, Wolpert DM: **The role of inertial sensitivity in**
• **motor planning.** *J Neurosci* 1998, **18**:5948-5957.

The kinematics of reaching movements was examined when a visual obstacle was set in three-dimensional space. The distribution of the near points, where the paths came closest to the obstacle, showed a strong anisotropy, clustering at the poles of a preferred axis through the center of the obstacle. The mobility minor axis, which represents the most inertially stable direction to a force perturbation, was not significantly different from the preferred near point axis. These results suggest that the dynamic characteristics of the arm are taken into account in the trajectory planning process.

74. Nakano E, Imamizu H, Osu R, Uno Y, Gomi H, Yoshioka T, Kawato M:
•• **Quantitative examinations of internal representations for arm trajectory planning: minimum commanded torque change model.** *J Neurophysiol* 1999, **81**:2140-2155.

As a computable version of the minimum motor-command change model, a minimum commanded torque change model was proposed and compared with other optimization models based on a large database of horizontal and vertical two-joint arm movements. The best performance of the model supports dynamic trajectory planning while taking into account not only environmental and link dynamics but also muscle dynamics.

75. Kawato M: **Trajectory formation in arm movements: minimization principles and procedures.** In *Advances in Motor Learning and Control.* Edited by Zelaznik HN. Illinois: Human Kinetics Publishers; 1996:225-259.

76. Soechting JF, Flanders M: **Movement planning: kinematics,**
• **dynamics, both or neither?** In *Vision and Action*. Edited by Harris LR, Jenkin M. Cambridge: Cambridge University Press; 1998:332-349.

The final posture of the arm in a reaching movement can be predicted according to a criterion that is related to energy expenditure, and the hand paths during planar arm movements can be at least partly predicted by another criterion (minimum muscle force change) that is also related to energy expenditure. The authors conclude that movement planning must involve dynamics.

77. Harris CM, Wolpert DM: **Signal-dependent noise determines**
•• **motor planning.** *Nature* 1998, **394**:780-784.

A unifying theory on trajectory formation of saccades and arm movements is proposed. It is assumed that the neural control signals are corrupted by noise, which increases with the size of the control signal. A simple principle to minimize the variance of the final eye or hand position could thus reproduce known invariant trajectory characteristics, Fitts' law, and the 2/3 power law. The final position error is the time integral of the noise in the motor command, which is filtered by time-variant linearized dynamics of the motor plant. In this interpretation, the minimum variance model could be viewed as a temporally weighted version of the minimum motor-command change model, because the noise variance is related to the square of the motor command.

78. Kawato M: **Bidirectional theory approach to consciousness.** In *Cognition, Computation and Consciousness*. Edited by Ito M, Miyashita Y, Rolls ET. Oxford: Oxford University Press; 1997:223-248.

79. Middleton FA, Strick PL: **The cerebellum: an overview.** *Trends Cog Sci* 1998, **2**:305-306. [Also published in *Trends Neurosci* 1998, **21**:367-368.]

80. Tamada T, Miyauchi S, Imamizu H, Yoshioka T, Kawato M: **Cerebro**
•• **cerebellar functional connectivity revealed by the laterality index in tool-use learning.** *Neuroreport* 1999, **10**:325-331.

It is known that the anatomical connections between the cerebral cortex and the cerebellar cortex are largely contralateral. Thus, if some area in the cerebral cortex is anatomically connected with some region in the cerebellar cortex, their bilateral activation patterns should be correlated. A new method to reveal cerebro-cerebellar functional connectivity was proposed while using the laterality index. It has been suggested that a posterior–superior fissure of the lateral cerebellum is involved in tool-use learning [42••]. Pars opecularis and pars triangularis were shown to be functionally connected with this part of the cerebellum. This is interesting because some theories advocate that language evolution is an extension of human tool usage capability.